GPS tracking of the foraging movements of Manx Shearwaters *Puffinus puffinus* breeding on Skomer Island, Wales

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We report the first successful use of miniature Global Positioning System loggers to track the ocean-going behaviour of a c. 400 g seabird, the Manx Shearwater *Puffinus puffinus*. Breeding birds were tracked over three field seasons during the incubation and chick-rearing periods on their foraging excursions from the large colony on Skomer Island, Pembrokeshire, UK. Foraging effort was concentrated in the Irish Sea. Likely foraging areas were identified to the north, and more diffusely to the west of the colony. No foraging excursions were recorded significantly to the south of the colony, conflicting with the conclusions of earlier studies based on ringing recoveries and observations. We discuss several explanations including the hypothesis that foraging may have shifted substantially northwards in recent decades. We found no obvious relationship between birds’ positions and water depth, although there was a suggestion that observations at night were in shallower water than those during the day. We also found that, despite the fact that Shearwaters can be observed rafting off-shore from their colonies in the hours prior to making landfall at night, breeding birds are usually located much further from the colony in the last 8 h before arrival, a finding that has significance for the likely effectiveness of marine protection areas if they are only local to the colony. Short sequences of precise second-by-second fixes showed that movement speeds were bimodal, corresponding to sitting on the water (most common at night and around midday) and flying (most common in the morning and evening), with flight behaviour separable into erratic (indicative of searching for food) and directional (indicative of travelling). We also provide a first direct measurement of mean flight speed during directional flight (c. 40 km/h), slower than a Shearwater’s predicted maximum range velocity, suggesting that birds are exploiting wave or dynamic soaring during long-distance travel.

**Keywords:** climate change, navigation, procellariiform, satellite telemetry, seabird.

Many procellariiforms have an inherently precarious life-history, with breeding concentrated at a relatively small number of islands or other isolated locations, coupled with central-place foraging strategies involving long-distance movements over the open ocean. Understanding their foraging movements is crucial to assessing their conservation status, and indirectly the health of the marine resources on which they depend, but their ocean-wandering lifestyle makes these hard to study with any precision. Satellite tracking has brought huge advances in our understanding of the precise foraging movements of larger species such as albatrosses, bringing into focus their vulnerability to modern fishing practices, but the size of loggers has precluded this for smaller species.
(reviewed in BirdLife International 2004). In this paper we report the first use of precision GPS logging technology to study the individual foraging movements during breeding of a 400 g procellariiform, the Manx Shearwater *Puffinus puffinus*.

Britain and Ireland hold the majority of the world population of Manx Shearwaters (Lloyd *et al.* 1991, Hamer 2003), with just two small Welsh islands, Skokholm and Skomer, holding in excess of 150,000 breeding pairs, a substantial proportion of the global breeding population (Smith *et al.* 2001). Manx Shearwaters, which shallow dive from the surface, predominantly for small clupeids and some squid (Thompson 1987, Brooke 1990), are known to fly considerable distances during the breeding season; for example, incubating birds of both sexes are away from the colony for an average of about a week at a time (Brooke 1990). Sea surveys have revealed that there are concentrations of birds at various places in the Irish Sea and its vicinity (Begg & Reid 1997). Distribution maps produced from such surveys are invaluable in pin-pointing the areas where the main feeding concentrations of seabirds occur. However, where there is more than one feeding concentration and more than a single breeding colony, they cannot shed light on the feeding ranges of the birds from the different colonies, nor on the foraging behaviour of individuals. Furthermore, in a species as long-lived as the Manx Shearwater, in any year possibly as much as half of the population are not breeding; these are mainly immature birds, not yet of breeding age (up to 7 years; Brooke 1990), but also include divorced or widowed birds searching for a new mate. While each of these birds (without breeding duties) will be associated with a particular colony, they may not return there with the regularity of breeders. Hence their foraging patterns at sea may well be different from those of breeders.

Early attempts to determine the foraging movements of breeding Manx Shearwaters involved interpretation of ringing recoveries, together with offshore and coastal sightings. These led to the hypothesis that many birds utilize the sardine fisheries originating in the Bay of Biscay, which move northwards up the bay during the northern summer (Lockley 1953). Lockley’s hypothesis implies a substantial long-distance southwards component to the Shearwater’s foraging movements. Later analyses, however (Perrins & Brooke 1976), found little support for this hypothesis. In this paper, we use miniature GPS loggers to track the movements of a number of breeding birds while they are away from Skomer Island, during both the incubation and the chick-rearing periods. This has allowed us to make a first direct test of the current validity of Lockley’s hypothesis, and to investigate in some spatial detail how breeding birds utilize marine resources accessible from their colony.

**METHODS**

**Subjects**

Between June and August, in the three seasons 2004–6, breeding birds were located in their burrows using call playback at two densely occupied sites on Skomer Island, Pembrokeshire, Wales (54°44′N 5°17′W): one close to the Warden’s House at North Haven (2004, 2005), the other close to the Old Farm (2006). Burrows were chosen for the accessibility of the nest chamber via the burrow entrance or an inspection hatch. In 2004, a small wire gate, with a one-way trip, was constructed in the mouth of each burrow to allow capture of returning birds, or, during incubation, retention of departing birds immediately after changeover. Frequent inspections (every 20–30 min) ensured that we were able to capture focal study birds by hand promptly. In 2005 and 2006, a simpler system of small marker pegs placed vertically in the entrance and frequent inspection (every 15–20 min) was used to identify the comings and goings of focal birds. To determine whether adults had fed at sea, we weighed them with a spring balance before and after each deployment where it was expedient and would cause minimal extra disturbance. Only birds weighing 400 g or more were fitted with trackers.

**GPS tracking**

The global positioning devices (GPDs, adapted from original designs by von Hünerbein *et al.* 2000, Steiner *et al.* 2000) consisted of an integrated GPS receiver, flash memory and ground plane (µ-blox Co., Thalwil, Switzerland), with 4 V, 150 mAh, lithium polymer rechargeable battery (Ultralife Batteries Inc., Newark, USA), and 12.5×12.5×3 mm ceramic insulated antennae (Compotron Ltd, Swindon, UK). Total active operation time was about 55 min. The GPDs were configured to attempt to obtain positional fixes for up to 200 s at 2-h intervals. This meant that, when successful, GPDs recorded a brief burst of positional fixes (at 1-s intervals) every 2 h, allowing the type and direction of movement to be determined, whilst maximizing the proportion of the foraging journey recorded. GPDs were then
waterproofed using lightweight heat-sealed plastic sleeves immediately prior to deployment. The GPDs (which had a flat, streamlined profile of $8 \times 30 \times 60$ mm and weighed c. 17 g including attachment material) were attached dorsally between the shoulders using three to five thin strips of black TESA marine cloth tape, each anchored beneath a small bunch of back feathers and closed over the top of the device (tape attachments have less impact than harnesses; Phillips et al. 2003). On return, the device was removed by peeling the tape away from the feathers and the bird was returned to its burrow. Data were downloaded onto a field laptop using proprietary µ-BLOX software and visualized and analysed using Fugawi, MatLab, and ArcGIS 9 software. A British Geological Survey DigBath250 data licence was purchased for conducting bathymetry analysis.

RESULTS

Effectiveness of the tracking technique

In total, we obtained 50 individual datasets of varying degrees of completeness, constituting a success rate of about 50% per deployment. Tracks were recorded from 34 different individuals. Eight birds were tracked twice, one bird was tracked three times and two birds were tracked on four occasions but across 2 years. No bird was tracked more than three times in a season. We obtained six tracks in 2004, five from chick-rearing birds; in 2005 we obtained 18 tracks, 16 from chick-rearing birds; and, in 2006 we obtained 26 tracks, 16 from chick-rearing birds. No tracked bird failed to return to its burrow. However, in many cases trackers failed to return to acquire positions, ran out of battery whilst the bird remained underground, returned waterlogged, or were lost at sea because the tape attachments eventually fail in seawater (an important welfare failsafe in case we did not manage to recapture the bird). The mean duration of the foraging trips studied was 71.8 h, but the distribution was heavily skewed, with 68% lasting just 1 or 2 days and the longest trip lasting 12 days. Mean recording duration of the devices was 31.2 h, so that most trips (69%) of 2 days or less were fully recorded, but only the early part of longer trips was recorded before the battery was exhausted. In all, 46% of all trips were recorded completely or almost so (up to 4 h before recovery), and 89% of all fix bursts contained fixes generated by four or more satellites, providing highly accurate position ($\pm c. 4$ m), speed and direction data.

Evidence for foraging

The duration of foraging excursions varies greatly in unmanipulated birds, especially with breeding stage and, to a lesser extent, sex. Nevertheless, trip durations can give an indication of whether our manipulated birds were indulging in normal foraging. Whilst a systematic comparison between manipulated and unmanipulated birds was not possible because we did not measure controls at the same time, the duration of tracked excursions was broadly consistent with previous observations. In our study, trips during incubation lasted a mean of 5.46 days ($\pm 0.92$ se, $n = 13$), and during chick feeding a mean of 1.65 days ($\pm 0.15$, $n = 37$). Brooke (1990) measured mean trip durations of 6.88 ± 0.29 for males and 5.42 ± 0.23 for females during later incubation (Skokholm 1975 and 1976 breeding seasons), and reported means of 1.63 days for males and 2.0 days for females during chick feeding (data from Rum, Thompson 1987). Gray and Hamer (2001, data from Skomer 1999) measured trips during chick feeding at 1.5 ± 0.2 sd days for males and 1.8 ± 0.2 sd days for females. In addition, in 33 cases (66%) there was clear evidence from an adult’s weight measured before and after deployment that it had fed during the tracked excursion. In 13 cases (26%), one or other adult measurement was missed and we were unable to judge. In four (8%) cases, a tracked adult was sufficiently lighter when weighed the second time that it is possible it had not fed (although in all four cases it is possible that it had fed its chick before we weighed it, and this accounted for the weight reduction). Hence, most or all trips tracked represent successful foraging excursions, and this also suggests that birds were able to cope with the drag or the increased wing-loading resulting from carrying the devices.

Distribution and direction of trips

All tracks recorded were plotted in Figure 1 to show the overall distribution of foraging movements during incubation and chick-rearing. Plotting the data as tracks connecting each approximately 2-h position estimate also allowed some visualization of any pseudoreplication effects (inherent in tracking data of this sort) in the following analyses. Nevertheless, it was clear that birds could travel long distances between each 2-h fix, and hence such fixes provided a powerful description of the overall distribution of the birds’ activity when away from the colony.
Foraging movements were concentrated northwards and westwards into the Irish Sea, and not southwards. This was true both during incubation (red), when birds were often away a week or longer, and during the shorter trips of chick-rearing birds (blue). Furthermore, birds did not frequent all areas within reach given the actual trip distances measured. Several areas of activity could be identified, with particularly dense activity around Skomer, in Cardigan Bay, and at locations in the Irish Sea further north (off Dundalk and the Mull of Galloway) and west of the colony. Though sample sizes between years were too small to determine definitively whether or not there were inter-annual effects, informal inspection suggests there was substantial overlap between locations visited in different years.

As the logging devices were programmed to obtain a short series or cluster of consecutive fixes at 1-s intervals during each 2-h duty cycle, we obtained not just a position every 2 h, but a snapshot of the bird’s movement behaviour (principally surface speed and direction of movement) at the same time. First, we assigned each cluster of fixes a single position represented by the median latitude and median longitude of the series, hereafter called simply a ‘location’, and plotted these for all excursions in relation to foraging trip length. Figure 2a shows that despite our being unable to track birds for the duration of longer trips, there was a clear tendency for longer trips to start in a more northwards direction. Removing all pseudo-replication effects by representing each trip with just a single location taken from the middle of the first day of the trip shows essentially the same result (Fig. 2b).

We then assigned an estimate of quality to each fix based on the number of satellites contributing to the fix. Our devices recorded fixes whenever three or more satellites were successfully accessed, but with only three satellites, a position fix can be several tens of metres off true position. This has no significance for the general location estimates presented here, but can greatly affect speed estimates derived from movement between fixes within a cluster. We therefore filtered the clusters by quality and calculated mean movement speeds (‘speed’) whenever there were sufficient fixes based on at least four satellites. Next, we used the data within each cluster to calculate both the direction of movement from one second to the next (‘direction’), and the variability in that direction across the cluster (‘directionality’ using the circular statistic $r$, measured from 0 to 1, where 1 equates to unidirectional and 0 equates to randomly oriented; Batchelet 1981). Directionality was then plotted in Figure 3 against speed, for every location.

Surface speeds were bimodal. We therefore fitted a mixture model of two Gaussian curves to the distributions shown, estimating the mean and variance of the two movement modes, which clearly correspond to locations where the bird was either sitting ($0.85 \pm 0.24 \text{ m/s}$) or flying ($11.13 \pm 9.55 \text{ m/s}$). The higher variance characteristic of the fast movement mode indicated that birds sometimes fly with the wind and sometimes against it, whereas sitting birds may drift with the current and probably make no attempt to counteract their drift. Nevertheless, the central tendency of the fast distribution provided a direct measure of flight speed, if we assume that into-wind and down-wind effects are roughly balanced across the dataset.
Figure 2. Locations classified by foraging trip length: (a) all locations plotted (white = 1 day, light grey = 2 days, dark grey = 2–4 days, black ≥ 4 days); (b) each excursion represented by a single location, that closest to 1300 h, and not outside 1100–1500 h, on the first day, to remove effects of pseudoreplication.

Figure 3. Gaussian mixture model of speeds during all fix clusters based on four or more satellites, overlaid on a scatter plot of speed against directionality for each location, with a box showing values taken to indicate ‘directional flight’ ($r > 0.85$). The optimal separation boundary between the two distributions is shown as a dashed line at 2.5 m/s.
Using the optimal separation boundary of the two fitted distributions (2.5 m/s) we classified each location as either sitting or flying with maximum probability. There was also considerable variation in directionality. For slow moving (sitting) birds, this variation was almost certainly attributable to increasing dominance of GPS position error as actual speed approaches zero, so it was ignored. For fast moving (flying) birds, variation in directionality allowed us to distinguish birds in strongly oriented flight, and therefore probably travelling, from those in erratic flight that were more likely to be involved in localized behaviour such as active searching for food. Informal inspection of the tracks suggested that below a threshold of about 0.85 (normalized directionality), birds were often involved in making major turns, whereas above this threshold flight paths showed undulations, perhaps indicative of wave- or shears-soaring, but no major alterations in overall orientation.

In an attempt to distinguish approximately localized activity (foraging, resting) from travelling behaviour, Figure 4 plots the locations assigned by whether birds are sitting or flying erratically (Fig. 4a), or flying directionally (Fig. 4b). Fix clusters that did not contain accurate position data were excluded. Figure 4 also plots the British Geological Survey DigBath250 bathymetric database for the Irish Sea to provide a detailed visualization of the birds’ activity in relation to underlying water depth.

The patchy distribution across the region clearly shows several important areas where activity is concentrated. Comparing the distributions suggests that activity on the water and erratic flight may have been more locally concentrated than travelling behaviour, although there was no clear separation in most areas. Around the colony itself, the concentration of activity could have been partially explained by birds waiting to come onshore (which they only do after dark) at the end of their fishing trips, or preparing themselves for a foraging trip immediately after leaving the colony. To remove activity specifically associated with leaving or returning to the colony, we plotted in Figure 5 the distribution of locations after removal of all points up to 8 h after deployment or 6 h before return.

Although several relatively shallow areas (e.g. Bristol Channel east of Lundy, and the area north and

![Figure 4](image_url). Locations, filtered for fix quality, classified as: (a) sitting (red points) or erratic flying (red arrows); or, (b) travelling (green arrows). Locations are overlain on bathymetry.
east of Anglesey) contained no activity, there was no clear overall relationship with water depth. Figure 6 (top two panels) compares the distribution of locations with, as a null hypothesis, a random distribution of points (not on land) generated for the area within the minimum convex polygon surrounding these observations. A Mann-Whitney $U$ test showed no significant difference between the depths of actual locations and randomly created locations ($Z = -1.09$, $n_{\text{random}} = 600$, $n_{\text{bird}} = 549$, $P = 0.28$). We then used time of Civil Twilight (U.S. Naval Observatory, Astronomical Applications Department website – http://aa.usno.navy.mil/faq/, accessed February 2008) for the actual times and dates of each observation to determine whether it was night or day, and segmented the data again by sitting versus flying. A Kruskal–Wallis test showed that the depth distributions differed significantly ($\chi^2 = 32.84$, d.f. = 3, $n_{\text{day}} = 458$, $n_{\text{night}} = 91$, $P < 0.001$), with night-time locations more likely to be shallow. Further post-hoc comparisons showed that there was a significant depth difference between night-time and day-time locations ($Z = 5.54$, $n_{\text{night-time}} = 91$, $n_{\text{day-time}} = 458$, $P < 0.001$), shown in the bottom two panels of Figure 6, but not between flying and sitting ($Z = -0.94$, $n_{\text{flying}} = 169$, $n_{\text{sitting}} = 380$, $P = 0.35$). It is important to remember that since each bird and each track contributed a series of locations within the actual data (though not the simulated random data) there was some inherent pseudoreplication in the tests. However, since locations within a bird’s track were always at least 2 h apart there was in general ample time for birds to have moved across the entire depth range between locations. Nevertheless, we followed the one significant result here with a more conservative Wilcoxon matched pairs test using a single day and a single night location (those closest to midday or midnight) for each track. Although the median depth difference was negative, and hence night locations were shallower than day, this was not significant ($U = 91.0$, $n = 23$ pairs, $P = 0.157$; median depth difference = $-14.74$ m).

We plotted flying versus sitting activity with time of day in Figure 7. There was a clear diurnal cycle. Sitting activity was approximately bimodal, with peaks during the night and in the middle of the day. Flying activity also appeared to be bimodal, with two peaks dovetailing quite well with the pattern of sitting activity. Finally, in an attempt to determine which locations were most used by birds in the hours before returning to the nest at the end of the foraging trip, we plotted activity distributions during the final 8 h before recovery (Fig. 8).

**DISCUSSION**

**Foraging movements during the breeding season**

Early attempts to determine the foraging movements of birds breeding in the Pembrokeshire colonies involved interpretation of ringing recoveries, together with off-shore and coastal sightings. Ringing recoveries led to the hypothesis that many birds utilize the sardine fisheries originating in the Bay of Biscay which move northwards up the bay during the northern summer (Lockley 1953). Later, Perrins and Brooke (1976) recognized that Lockley had underestimated the age at first breeding, and applied more stringent criteria for whether birds recovered in Biscay were likely to be breeders. They found no evidence for foraging excursions this far south after laying, and suggested that from the breeding population only females absent from the colony for the 2 weeks or so
of egg formation were likely to make the journey to Biscay. Because departure from the burrow of such ‘honey-mooning’ females is unpredictable, we were not able to track such birds using GPS and so this hypothesis remains untested. Nevertheless, Lockley (1953) also reported observations of mass bird movement off-shore and particularly past the headlands of Cornwall and Finistere (which he termed the ‘Manx Seaway’). Although the Manx Seaway was reportedly less intense in June and July than in April and May, it still appears to provide evidence for a substantial long-distance southwards component to the Pembrokeshire birds’ foraging movements even long after laying. Our findings are strikingly at odds with this. We found no evidence for southerly foraging excursions other than very locally, even when birds were absent from their burrows for many days. As we were unable to track birds for more than the first day or two of each excursion, we cannot know exactly what happens beyond this time on longer journeys. Nevertheless, Figure 2 shows that there was a strong tendency for birds to start heading in a northerly, and to a lesser extent westerly, direction when they were embarking on what turn out to be longer journeys. It is possible that southerly movements might have been observed had we tracked birds earlier during incubation (our tracks of incubating birds are from late June and July), but Lockley still reported strong southwards mass movements along the Manx Seaway during July, and this does not

Figure 6. Histogram of locations with depth. Random and actual locations are compared (top two histograms), and actual locations, classified as light or dark using nautical night-time, are compared in the bottom two histograms. Note that there are fewer night-time observations because the night is very short at these latitudes during summer.
match our findings. Even our earliest birds did not fly southwards. There would appear to be three feasible explanations.

First, southwards moving birds may be non-breeders. Up to half of the birds ‘belonging’ to the colonies were immature, partnerless, or failed breeders. Presumably, such directional specialization would require either that breeders and non-breeders seek different resources, or that breeders lack time between nest-tending duties to fly sufficiently far south to exploit the sardine fisheries. In this latter case, we expect that non-breeders’ excursions could be longer than those of breeders, but this has never been measured.

Secondly, if there is strong local partitioning in the Pembrokeshire colonies, and sub-colonies utilize their own resource areas, then it might be possible that our samples of breeders happen to be taken from two areas that only forage to the west and north. A division between the neighbouring islands of Skomer and Skokholm is a related possibility, but the exchange of ringed birds between the two (Brooke 1990) suggests that mixing across the colonies might make the formation of stable and different traditional foraging routes unlikely. At present, data are too sparse to test this interesting possibility.

Thirdly, the species’ foraging ecology may have changed in the half century since Lockley’s observations, and the birds are no longer utilizing foraging grounds to the south. Contemporary headland sightings could potentially address this hypothesis. Certainly, Brooke’s (1990) analysis of ringing recoveries since

Figure 7. A histogram showing the frequency of locations containing flying and sitting activity over the 24-h period.

Figure 8. A plot of locations before birds arrive onshore at the end of their foraging trip (white 0–2 h before arrival, light grey 2–4 h before arrival, dark grey 4–6 h before arrival, black 6–8 h before arrival).
the 1940s suggested that birds were even then penetrating less far south than in Lockley's time, and it is possible that this trend has continued. Nevertheless, if a northwards shift has occurred, perhaps because of warming seas, then it is surprising that we found no evidence of excursions further north than the Mull of Galloway, which is about the limit of northwards movement proposed by Lockley on the basis of his original data. As the Pembrokeshire population is probably increasing, we should expect to see a dramatic increase in the density of birds in the Irish Sea if they are no longer travelling south, and still travelling no further north.

**Activity within the Irish Sea**

Within the Irish Sea itself, observations at sea (e.g. Pollock et al. 1997) have shown that Manx Shearwaters are not particularly abundant in March and April, become more common during May and June, and peak during July and August. Although hard to generalize, the peak numbers tend to occur in the south Irish Sea (including Cardigan Bay and extending as far west as the south-eastern tip of Ireland), in the North Channel (Mull of Kintyre to Mull of Galloway) and in the Irish Sea close to the Irish coast from about Dublin north to Dundalk (c. 53°15′N to 54°0′N). The first two of these are close to breeding colonies (Pembrokeshire islands and Copeland, respectively) and may, at least in part, be associated with local movements of birds from these populations. The third is in some ways of more interest because there are no significant colonies nearby: Bardsey with about 7000 pairs is the nearest; the colony on the Calf of Man is insignificant (Newton et al. 2004). Yet throughout the summer, large numbers of birds are found in this area and high numbers are maintained into September, even after the numbers at the colonies (and the two other sites of concentration mentioned above) have started to diminish. This area lies to the north and west of the Irish Sea front (Pollock et al. 1997) where high seabird density has been observed (Begg & Reid 1997), presumably in response to high marine productivity associated with the sea front and the stratified waters west of it.

Our tracking data matched these distributions well, demonstrating that birds breeding at the Pembrokeshire colonies are likely to be a major contributor to these observed concentrations. The distributions of birds on the sea or in non-directional flight, activities most likely to be associated with feeding, were clearly concentrated in these three areas (see Fig. 4), whilst birds in travelling flight showed a less concentrated distribution. The concentration in Cardigan Bay was sufficiently close to Skomer to be in range for birds waiting to come ashore at night. Nevertheless, considerable activity here remained even if we excluded activity in the 8 h after deployment and 6 h before return (Fig. 5). It is most likely therefore that Cardigan Bay is also an important foraging destination. In fact, Figure 5 also shows that many birds not about to make landfall, and therefore presumed to be engaged in foraging activity, could also be found relatively close to the colony, and to the west in particular, suggesting that the colonies are themselves located close to another important foraging area, possibly associated with the Celtic Sea Front (Pollock et al. 1997). In contrast, in the final 8 h prior to returning from a foraging trip, birds were to be found not only concentrated close to the island, but also dispersed much further afield, until very close to the time of making landfall (Fig. 8).

**Diurnal activity patterns**

Birds were most likely to be recorded in flight in the morning from around dawn until around 10:00 h, and then again, less obviously, during the afternoon and early evening. Perhaps the most obvious explanation for this is that they were commuting between fishing and rafting areas in the morning and evening, and then sitting at night and fishing in the middle of the day. Inspection of the spatial distribution of recorded positions during actual subjective daylight and darkness suggests that night-time activity is more clustered than day-time activity. Furthermore, whilst there was no obvious overall relationship with water depth, other than an apparent avoidance of shallow areas in the Bristol Channel and north of Anglesey, there was a suggestion of a shift from deeper to shallower water at night.

**Flight parameters**

The mean surface speed for our birds showing directional travel was about 11 m/s (40 km/h), which is slightly slower than, but still in reasonable agreement with, earlier estimates of flight speed derived from observation (approximately 40–55 km/h, Lockley 1953). Calculation suggests that Vmp (minimum power velocity) should be about 7.5 m/s (27 km/h) and Vmr (maximum range velocity) about 14 m/s (50 km/h) for the Manx Shearwater (Pennycuick 1969), so we suggest that birds are flying in the
middle of their theoretical speed range for purely powered flight. As long-distance movement might be expected to favour flying close to Vmr, it seems likely here that birds may be flying closer than expected to Vmp as they exploit non-powered flight advantages in the form of wave or dynamic soaring. Birds flying north to the Mull of Galloway to feed travelled a straight-line distance from Skomer of more than 330 km each way, involving a total predicted minimum direct commuting flight time of around 16.5 h. This foraging area is much closer to other breeding colonies, most notably Copeland situated about 30 km away. The foraging destinations of Copeland birds are currently unknown, but it seems that they would stand to gain a 15-h (600 km) travelling advantage over Pembrokeshire birds by utilizing the Mull of Galloway area. The second major northerly foraging area is also approximately 75 km closer to Copeland than Skomer, again giving a potential 3.75 h travelling advantage to Copeland birds. Such an advantage might be expected to result in increased provisioning and higher breeding success.

**Significance for conservation at sea**

The Birds Directive (79/409/EEC) requires each member state of the EU to set up marine special protection areas to protect birds, such as the Manx Shearwater, that are considered rare or vulnerable within the European Community. Such seabirds have two key requirements: safe nesting sites and safe and food-rich feeding. The former are, in some ways, easier to provide; most current large colonies are designated nature reserves where people are on high alert for threats, particularly those from introduced mammalian predators. Even some formerly successful colonies, such as Lundy and Canna, where rats have almost exterminated the birds, have recently been cleared of these predators and may become thriving colonies again.

The provision of safe feeding areas at sea is, however, much more difficult. Our findings emphasize the problems associated with trying to provide these places for such wide-ranging species. Marine Nature Reserves provide some protection for the birds when they are immediately offshore. In the case of the Manx Shearwater, these are mainly beneficial to evening assemblies of birds waiting to come onshore. Our data indicate that the majority of the breeding adults may not join these assemblies, being much farther from the colony when dusk falls (Fig. 8), although it is important to consider that birds carrying trackers may have behaved differently to unmanipulated birds and may therefore have reached the vicinity of the colony later on their day of return, simply because they were carrying an additional encumbrance. Further, as with most other seabirds, the areas used for feeding are much more distant from the colony and more diffuse, making it difficult or impossible to provide them with anything near complete protection while they are foraging. The future conservation of vulnerable species with such wide-ranging habits as the Manx Shearwater will require a fuller understanding of the areas of sea they use and this will require integrating movement and activity information from a variety of techniques, including precision GPS tracking. Further, we should not ignore the possibility that resources, and hence resource use, may be changing.

**Impacts of tracking on behaviour**

The Manx Shearwater is currently one of the smallest seabirds to have been tracked using GPS technology. We deployed the smallest devices available, used the generally agreed lowest impact attachment methods (e.g. Phillips et al. 2003), and restricted deployments to single excursions (occasionally, with one or more subsequent deployments only after an interval). At approximately 4% body weight, and with a very low profile, we believe our devices deployed in this way had minimal lasting impact. It is of course possible that behaviour during tracked excursions was not fully representative of normal behaviour, and this caveat must always be considered when drawing inferences from this and similar data. Telemetry advances are revolutionizing the study of wild birds, but improvements must always strive to reduce impact both for ethical reasons and so that data remain representative of normal behaviour.

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